Resistance to *Rhopalosiphum padi* (Homoptera: Aphididae) in Three Triticale Accessions

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ABSTRACT Experiments were conducted to identify and characterize host plant resistance to bird cherry-oat aphid, *Rhopalosiphum padi* (L.), in various wheat and wheat–grass hybrids. Initial tests screened for resistance to *R. padi* among 12 grass accessions (eight wheat [*Triticum aestivum* L.], three triticale [X*Triticosecale* Wittmack], and 1X*Elytricum* [*Elytrigia elongata* [Host] Nevski × *Triticum aestivum* hybrid]). *R. padi* had less population growth on triticale accessions '8TA5L' (PI 611760) and 'Stniism 3' (PI 386156) than on other accessions, but nymphiposition by *R. padi* did not differ among the 12 accessions. Follow-up experiments were conducted to characterize antibiosis, antixenosis, and tolerance to *R. padi* in three wheat and three triticale accessions. In antibiosis experiments, Stniism 3 and triticale 'H7089-52' (PI 611811) prolonged time to reproduction by *R. padi* compared with that on wheat accessions 'Arapahoe' (PI 518591), 'KS92WGRC24' (PI 574479), and 'MV4' (PI 435095), whereas time to reproduction on 8TA5L was intermediate and did not differ from that on the other five accessions. Also, *R. padi* produced fewest progeny on Stniism 3, and fewer progeny on 8TA5L than on H7089-52, Arapahoe, KS92WGRC24, and MV4. Stniism 3 showed antixenosis, because fewer winged *R. padi* selected Stniism 3 than Arapahoe, H7089-52, or MV4 in choice tests. In tolerance experiments, a 300 aphid-day infestation of *R. padi* limited shoot length of Arapahoe and KS92WGRC24 plants. Shoot lengths did not differ between infested and noninfested seedlings of MV4, 8TA5L, H7089-52, and Stniism 3, indicating tolerance to *R. padi* in these accessions. Triticale accessions 8TA5L, H7089-52, and Stniism 3 and MV4 wheat may be meaningful sources of *R. padi* resistance for small-grain breeding programs, and Stniism 3 may be particularly valuable, given reports of its additional resistance to the Russian wheat aphid, *Diuraphis noxia* (Mordvilko).

KEY WORDS *Rhopalosiphum padi*, PI 386156, PI 611811, antibiosis, tolerance

BIRD CHERRY-OAT APHID, *Rhopalosiphum padi* (L.) (Homoptera: Aphididae), is a nearly worldwide aphid pest of small grains (Elliott et al. 1994, Blackman and Eastop 2000). It is usually part of a complex of cereal aphids that infests small grains, and *R. padi* can often be the dominant cereal aphid species (Leather et al. 1989, Elliott et al. 1994, Morrill 1995). Infestations of *R. padi* and other cereal aphids cause yield loss to small grains by reducing particular components such as numbers of spikelets and seeds (Pike and Schaffner 1985, Kieckhefer and Gellner 1992, Kieckhefer et al. 1995). *R. padi* and several other cereal aphid species are vectors of barley yellow dwarf virus (BYDV), which can cause disease and further yield loss in small grains (McGrath and Bale 1990, Bauske et al. 1997, Herbert et al. 1999, Riedell et al. 1999, Chapin et al. 2001).

Limiting cereal aphid infestations can prevent damage, reduce incidence of BYDV, and sustain yield of small grains (Wiktelius and Pettersson 1985, Power and Gray 1995). Cereal aphid infestations may be limited by various chemical, biological, and cultural control strategies (Morrill 1995, Holtzer et al. 1996, Brewer and Elliott 2004). Host plant resistance is a desirable strategy for limiting aphid infestations because it is economical and environmentally sound (Panda and Khush 1995, Webster and Kenkel 1999).

Antixenosis, antibiosis, and tolerance are three modalities of host plant resistance (Painter 1951, Kogan and Ortman 1978, Panda and Khush 1995). Antixenosis and antibiosis are measured in terms of aphid responses to host plants, whereas tolerance is measured as differential responses among host plants to particular levels of aphid infestation. Antixenosis deters or reduces colonization by insects, and antibiosis causes adverse effects on insect life history. Tolerance is the ability of a plant to grow and reproduce despite supporting an infestation that would limit growth and reproduction of a susceptible host.

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Table 1. Small grain accessions used in host plant resistance experiments with *R. padi*

Plant taxon	Accession	Plant introduction no.	Reference
T. aestivum (wheat)	2137	PI 592444	Sears et al. (1997)
	AC Readymade	None	
	Alliance	PI 573096	Baenziger et al. (1995)
	Arapahoe	PI 518591	Baenziger et al. (1989)
	Capest	PI 324530	
	KS92WGRC24	PI 574479	Martin and Harvey (1994)
	MV4	PI 435095	Papp and Mesterházy (1993)
	Strampelli	PI 369727	
X*Triticosecale* (triticale)	H7089-52	PI 611811	
	8TA5L	PI 611760	
	Stniism 3	PI 386156	Nkongolo et al. (1996)
X*Elytricum* (wheat–grass)	Sando Selection (SS) 705	PI 604902	

Various forms of resistance to *R. padi* and other cereal aphids have been identified in wheat, *Triticum aestivum* L. (Smith et al. 1999); barley, *Hordeum vulgare* L. (Porter et al. 1999); and related grasses (Weibull 1988, Tremblay et al. 1989, Shukle and Quiroz 1994). However, relatively little has been published in regard to testing of rye, *Secale cereale* L., and wheat × *Secale* spp. hybrids (i.e., triticale, X*Triticosecale* Wittmack) against *R. padi.* Kieckhefer and Kantack (1988) found that yield losses in 'Cougar' rye were lower than those in 'Rough Rider' winter wheat when each was infested with comparable numbers of *R. padi.* Kieckhefer and Thysell (1981) screened 20 triticale lines against *R. padi* and found few differences in the number of *R. padi* progeny among accessions, with responses of none of the accessions differing from that of control CItr 666 barley. Antixenosis to winged *R. padi* was weak or absent in seedlings of the 20 triticale accessions.

In contrast, several accessions of rye and triticale have been identified as sources of resistance to other cereal aphids, particularly greenbug, *Schizaphis graminum* (Rondani), and Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Livers and Harvey 1969, Wood et al. 1974, Webster and Inayatullah 1984, Frank et al. 1989, Nkongolo et al. 1989, Webster 1990, Scott et al. 1991, Formusoh et al. 1994, Porter et al. 1994). Given the success against other cereal aphids and limited testing against *R. padi*, more testing of rye and triticale for resistance to *R. padi* is warranted. This article reports the results of tests to identify and characterize resistance to *R. padi* in three triticale accessions.

Materials and Methods

Experiments. Four experiments were conducted to identify and categorize resistance to *R. padi* among wheat and wheat–grass hybrids. The first experiment compared nymphiposition and population growth of *R. padi* among accessions and was used to identify resistance within ad hoc groups of eight wheat and three triticale accessions, and one accession of X*Elytricum* (wheat × *Elytrigia elongata* [Host] Nevski hybrid) (Table 1). 'Arapahoe' wheat was the susceptible control in all experiments, because it has been a widely grown cultivar in the northern Great Plains and

has shown no resistance to *R. padi* (Hesler et al. 1999). The last three experiments were conducted to characterize antibiosis, antixenosis, and tolerance to *R. padi* in three wheat and three triticale accessions that had limited *R. padi* population growth in the first experiment. Antibiosis among accessions was evaluated by measuring the developmental time of *R. padi* and number of progeny produced during the first 7 d of *R. padi* adulthood. Antixenosis was measured in a choice test of host selection among accessions by *R. padi.* Tolerance to *R. padi* was evaluated by comparing shoot growth among infested and noninfested accessions. All experiments were conducted at the Northern Grain Insects Research Laboratory, Brookings, SD.

Aphid Culture. All *R. padi* used in the experiments were obtained from a virus-free, multiclonal stock colony maintained on 'Hazen' barley (PI 483238) plants in growth chambers (20°C, photoperiod of 13:11 [L:D] h) in the laboratory. The colony of *R. padi* was established by collecting aphids from a wheat field in Brookings County, South Dakota, in summer 2001. Field-collected adult *R. padi* were placed in small (2 cm in diameter, 2 cm in length) cages described by Kieckhefer and Derr (1967) that held a 20% sucrose solution in sachets of Parafilm (American National Can Co., Greenwich, CT) membranes. Caged aphids were checked every few hours, and neonate offspring deposited within the first 30 h were transferred to noninfested plants (Kieckhefer and Gellner 1992). This procedure was repeated once or twice per year with colony aphids to ensure they remained free of BYDV, and colony plants were checked weekly to ensure they were free of BYDV symptoms. The colony was perpetuated by regularly infesting 2-wk-old barley plants with winged *R. padi.* Winged viviparae were used to initially infest plants in the first three types of experiments, and wingless aphids were used in the tolerance experiment. All *R. padi* used for infesting experimental plants were taken from colony plants initially infested 21–27 d earlier.

Plant Culture. All experimental plants were prepared by germinating seeds in the dark between layers of moist paper towels held in plastic containers (Hesler et al. 1999). After 24–48 h at 20°C, individual seedlings exhibiting uniform root and coleoptile

growth were planted into a 2:1:1 mixture of Vienna soil (fine-loamy, mixed Calcic Hapludolls), perlite, and coarsely ground coconut shells (Coir; J. R. Johnson Supply Inc., Roseville, MN). Seven-day-old seedlings were used at the start of each experiment; these seedlings had one fully extended leaf and a second leaf emerging from the whorl.

Screening Tests: Nymphiposition and Population Growth. Nymphiposition and population growth of *R. padi* were measured among the 12 grass accessions. The 12 accessions were divided into three ad hoc groups for testing, and groups were limited to a maximum of six accessions due to space and labor constraints. The first group included wheat accessions Arapahoe, '2137', 'AC Readymade', 'Alliance', and 'KS92WGRC24' and triticale accession '8TA5L'; the second included Arapahoe, 8TA5L, triticale accession 'H7089-52', and the X*Elytricum* accession 'SS 705'; and the third included wheat accessions Arapahoe, 'Capest', and 'Strampelli' and 'Stniism 3' triticale. Tests of the second and third groups were each repeated once.

Tests were set up by planting individual seedlings that exhibited uniform root and coleoptile growth in cylindrical tubes (D40 Deepot Cell, 6.4 cm in diameter, 25.0 cm in height.; Stuewe and Sons, Corvalis, OR) filled with soil mix and covered with 2.5 cm of 40-mesh sand. Each test was run in a growth chamber at 20°C, ≈40% RH, and a photoperiod of 13:11 (L:D) h. For each test, plants were randomized by accession within blocks with 8–12 replications. Seven-day-old plants were infested with three winged *R. padi* and then covered with vented, clear plastic cylinders (3.5 cm in diameter, 35 cm in height). Twenty-four hours after infesting, winged *R. padi* were removed, and the numbers of nymphs deposited per plant were counted (day 1 counts). Nymphs were thinned to five per plant, and infested plants were returned to the growth chamber. Twelve days later, the numbers of aphids per plant were counted (day 13 counts). For the first group of accessions, which was tested only once, day 1 and day 13 counts were each subjected to an analysis of variance (ANOVA) (PROC GLM, SAS Institute 1999), with the residual used as the error term and accession means separated by Fisher (1935) protected least significant difference (LSD) test ($P < 0.05$). For the second and third groups of accessions, which were tested twice, day 1 and day 13 counts were each subjected to ANOVA by using a mixed model (PROC MIXED, Littell et al. 1996), with accession as a fixed factor, test and block as random factors, and block nested within test. Accession means were estimated and separated by use of the least square means procedure (LSMEANS feature, Littell et al. 1996).

Antibiosis Tests: Developmental Time and Reproduction. Based on results of the previous tests, follow-up experiments were conducted to determine effect of selected accessions on the number of days from birth to onset of reproduction by *R. padi* and number of nymphs produced by individual *R. padi* in the first 7 d of adulthood. Three wheat accessions (Arapahoe, KS92WGRC24, and 'MV4') and the three triticale ac-

cessions (8TA5L, H7089-52, and Stniism 3) used in the previous screening tests were evaluated. MV4 has shown low levels of antibiosis to *R. padi* (Hesler et al. 1999), and it was used as an *R. padi*-resistant control. The accession KS92WGRC24 was included as an additional comparison because of its resistance to *D. noxia* (Martin and Harvey 1994). Seedlings exhibiting uniform root and coleoptile growth were planted individually into 10-cm-diameter clay pots filled with soil mix, and the soil mix was covered with ≈2.5 cm of 40-mesh sand. Each pot contained one seedling of a single accession. Eight pots of each accession were selected for uniformity of seedling growth 7 d after planting. Each plant was then infested with a winged *R. padi* and covered with vented plastic tubular cages (7 cm in diameter, 35 cm in height) pushed into the soil. After 24 h, aphids were thinned to one neonate per seedling. Each nymph–plant pair represented one replication. Pots were arranged in a randomized block design within a growth chamber (18–20°C, photoperiod of 13:11 [L:D] h). Beginning 6 d after initial infestation, experimental plants were checked daily for nymphiposition. The date when nymphiposition began was noted for each aphid, and neonates were counted and removed every 1–2 d over the next 7 d. The number of nymphs deposited by each aphid was summed over its first 7 d of reproduction. Two identical rounds of this experiment were performed. Data on time to reproduction from the two rounds were combined in one analysis, and data on number of progeny in a separate analysis. For each analysis, accession effect was tested using a mixed model ANOVA (PROC MIXED, Littell et al. 1996), with accession as a fixed factor, round and block as random factors, and block nested within round. After testing its associated variance for 0, the round × accession interaction was pooled into the error term. Accession means were estimated and separated by use of the least square means procedure with a Tukey–Kramer adjustment (LSMEANS, Littell et al. 1996).

Antixenosis Test: Host Selection. Differential host selection by winged adult *R. padi* was tested among the same three wheat (Arapahoe, KS92WGRC24, and MV4) and three triticale accessions (8TA5L, H7089-52, and Stniism 3) used in the antibiosis experiment. A choice test was set up in which winged viviparous adults were released, and the number that settled on plants of each accession after 48 h was counted. The test was performed three times. Experimental plants were prepared by sowing one germinating seed of an accession into a plastic 50-ml centrifuge tube (Cole-Parmer Instrument Co., Vernon Hills, IL) nearly full with soil mix. Seeds were covered with ≈2.5 cm of 40-mesh sand and gently watered. Upon seedling emergence, tubes were placed in a rack in descending order of seedling height. Seedlings were kept in a greenhouse (19°C, 57% RH, photoperiod of 13:11 [L:D] h) until they were used in the choice tests. One day before infesting, one plant of each accession was grouped with a seedling of similar height of each of the other accessions. The six tubes within each group were randomized by accession and placed upright and equi-

distant from one another in a circle within a 10-cm-diameter clay pot, which contained 7.5 cm (depth) of soil mix. Tubes were carefully placed such that their brims were even with the brim of the pot, and pots were filled with sand. Each pot was treated as a replicate block.

Heights of experimental plants were measured just before infesting with 60 winged *R. padi.* Winged *R. padi* were collected by aspirating them from sides of colony cages or by aspirating those that had fallen onto a white laboratory countertop after gentle shaking of colony plants. Thirty 30 alatae at a time were aspirated into glass vials (23 cm in diameter, 85 cm in height) and visually checked to ensure their viability. Two sets of 30 alatae were released in tandem into the center of each circle of test plants. A cylindrical cage (10 cm in diameter, 40 cm in height) was placed over each group of experimental plants immediately after adding alatae. Pots with caged plants were arranged in a circle within a growth chamber (20°C, ≈50% RH). The inside of the chamber was kept dark to preclude artifactual orientation of aphids to test plants in response to light (Webster and Inayatullah 1988).

After 48 h, pots were removed from the chamber, and winged *R. padi* were counted on each plant. The number of winged *R. padi* per accession was divided by the total number recovered per pot to calculate the proportion that chose each accession. Pots with <48 winged *R. padi* on test plants may have indicated some problem in aphid or plant viability, and such pots were eliminated from the experiment. This left seven of 12 in the first choice test, nine of 11 replicate pots in the second, and all 12 pots in the third test. Replicates with 48 or more winged *R. padi* from the three tests were combined into a single frequency table for χ^2 analysis (PROC FREQ, SAS Institute 1999). Proportions of aphids were tested for accession-by-replicate heterogeneity, followed by a test for accession effect on counts pooled across replicates (Zar 1996). A Tukey-type multiple comparison test for proportions was performed to separate accession means (Zar 1996). After counting winged aphids on test plants, the height of each plant was measured and shoots were clipped at soil level. Shoots were rinsed free of aphids, dried in an oven, and weighed. Correlation tests were conducted respectively between proportion of aphids per plant versus plant height (mean of 0- and 48-h measurements) and dry weight (second and third tests only) to determine whether host selection by winged *R. padi* was associated with these plant growth parameters (PROC CORR, SAS Institute 1999).

Tolerance Test: Shoot Growth. Tolerance was evaluated among accessions in a split-plot experiment. A 300 aphid-day treatment of *R. padi* was used to challenge seedling test plants (Kieckhefer and Gellner 1992). The experiment was set up using a split-plot design with six replicate blocks. The six test accessions (Arapahoe, KS92WGRC24, and MV4 wheat and 8TA5L, H7089-52, and Stniism 3 triticale) occurred in each of two groups per block. One group received the 300 aphid-day treatment, and the other received no aphids. The 300 aphid-days were applied to individual seedlings over a 7-d period by initially infesting with 30 moderate-sized *R. padi* nymphs (generally third to fourth instars), increasing to 40 aphids per plant on day 3, 50 aphids starting on day 5, and 60 aphids per plant on day 7. Infestations were checked daily, and aphids were added or removed to attain the target infestation level. Shoot lengths of individual seedlings (in centimeters) were measured from soil level to the tip of the longest leaf just before initial infestation and again after 7 d of infestation. The difference in shoot length between the start and end of the infestation period was used as a dependent variable to test for tolerance with a mixed model that included accession, infestation level, and accession-by-infestation interaction as independent class variables (PROC MIXED feature, SAS Institute 1999). The experiment was run twice, and data from the two runs were combined into a single ANOVA model, with accession treated as a fixed factor and experiment, block, and infestation-by-block as random factors. Accession effect was tested by using an error term pooled from the accession-by-experiment and accession-by-block within experiment terms, and aphid infestation effect and the accession-by-infestation level interaction were tested with an error term derived by pooling the experiment-by-infestation level term with the infestation level-by-block within experiment term. A significant accession-by-infestation level interaction ($P < 0.05$) would indicate that accessions responded differently in shoot growth to aphid infestation. Accession-by-infestation level means were estimated by calculating least-square means and separated by using a Tukey–Kramer adjustment (LSMEANS feature, Littell et al. 1996).

Results

Screening Tests: Nymphiposition and Population Growth. Nymphiposition by winged *R. padi* did not differ ($P > 0.05$) among accessions (first test: $x = 20.3 \pm 0.7$ nymphs per plant; df = 5, 44; $F = 2.01$; second test: $x = 11.1 \pm 0.5$ nymphs per plant; df = 3, 60; $F = 0.48$; and third test: $x = 11.6 \pm 0.4$ nymphs per plant; df = 3, 91; $F = 1.80$). However, *R. padi* population growth over 13 d differed ($P < 0.01$) in each of the three tests (first test: df = 5, 42; $F = 3.98$; second test: df = 3, 19.7; $F = 11.11$; and third test: df = 3, 45; $F = 14.94$). In the first test, 8TA5L triticale had fewer *R. padi* per plant than wheat accessions 2137, AC Readymade, Alliance, KS92WGRC24, and Arapahoe, which did not differ from one another in the number of *R. padi* per plant (Table 2). In the second test, 8TA5L had fewer *R. padi* per plant than Arapahoe or X*Elytricum* accession SS 705; H7089-52 triticale had fewer *R. padi* than SS 705. In the third test, Stniism 3 triticale had fewer *R. padi* per plant than the wheat accessions Arapahoe, Capest, and Strampelli, which did not differ from one another in number of *R. padi* per plant. Accessions 8TA5L and Stniism 3 produced moderate reductions in *R. padi* population growth and, because of this, were advanced for further testing. However, accession H7089-52, which showed only slight, nonsignificant reductions in *R. padi* population

Table 2. Screening tests: number of *R. padi* (mean ± SEM) on various wheat and triticale accessions after 13 d

Accession	Mean no./plant ± SE
First test group	
2137 wheat	131.9 ± 8.9a
8TA5L triticale	99.4 ± 14.2b
AC Readymade wheat	146.0 ± 9.2a
Alliance wheat	149.8 ± 10.4a
Arapahoe wheat	151.4 ± 10.4a
KS92WGRC24 wheat	153.8 ± 8.2a
Second test group	
8TA5L triticale	136.9 ± 8.2c
Arapahoe wheat	166.6 ± 7.1ab
H7089-52 triticale	145.8 ± 8.9bc
SS 705 X*Elytricum* wheatgrass	171.3 ± 4.2a
Third test group	
Arapahoe wheat	166.4 ± 16.1a
Strampelli wheat	152.8 ± 6.4a
Capest wheat	150.1 ± 11.5a
Stniism 3 triticale	76.6 ± 8.5b

For each test, means ± SEM not followed by the same letter are not significantly different (first test, LSD method; second and third tests, LSMEANS method; Littell et al. 1996; $\alpha = 0.05$). Means ± SEM in first group are for a single test ($n = 10$); those of second and third test represent two identical rounds of each test ($n = 16$).

growth compared with Arapahoe, also was included for comparison in further testing as a triticale with relatively little or no effect on *R. padi.*

Antibiosis Tests: Developmental Time and Reproduction. Triticale accessions Stniism 3 and H7089-52 prolonged time to reproduction by *R. padi* compared with that on wheat accessions Arapahoe, KS92WGRC24, and MV4, whereas time to reproduction on 8TA5L triticale was intermediate and did not differ from that on the other five accessions (Table 3; $F = 6.64$; df = 5, 121; $P < 0.001$). Also, *R. padi* produced fewest progeny on Stniism 3, and fewer progeny on 8TA5L than on H7089–52, Arapahoe, KS92WGRC24, and MV4 (Table 3; $F = 32.70$; df = 5, 119; $P < 0.001$). The number of progeny produced by *R. padi* on H7089-52 and KS92WGRC24 did not differ from that on 8TA5L, MV4, or Arapahoe.

Antixenosis Test: Host Selection. Fewer winged *R. padi* selected Stniism 3 triticale than Arapahoe and MV4 wheat and H7089-52 triticale (Table 4), based on data pooled across replicates ($\chi^2 = 15.2$, df = 5, $P < 0.01$). Host selection of KS92WGRC24 wheat and 8TA5L triticale was intermediate to and did not differ

Table 3. Antibiosis tests: days to reproduction and number of progeny produced by *R. padi* on various wheat and triticale accessions

Accession	Days to reproduction	No. progeny produced in 7 d
Arapahoe wheat	9.1 ± 0.1a	43.3 ± 1.1a
8TA5L triticale	9.2 ± 0.1ab	34.9 ± 1.1b
H7089-52 triticale	9.7 ± 0.1b	39.1 ± 1.0ab
KS92WGRC24 wheat	8.9 ± 0.1a	39.2 ± 1.0ab
MV4 wheat	9.0 ± 0.1a	40.7 ± 1.1a
Stniism 3 triticale	9.7 ± 0.2b	23.6 ± 1.9c

Data are means ± SEM. Those within a column not followed by the same letter are significantly different ($\alpha = 0.05$, LSMEANS method; Littell et al. 1996). Means are for two identical tests ($n = 15$).

Table 4. Antixenosis test: proportion of alate *R. padi* selecting wheat and triticale accessions after 48 h

Accession	Mean ± SD
Arapahoe wheat	18.2 ± 6.0a
H7089-52 triticale	18.1 ± 5.9a
MV4 wheat	17.6 ± 8.0a
8TA5L triticale	17.1 ± 5.9ab
KS92WGRC24 wheat	15.0 ± 5.3ab
Stniism 3 triticale	13.9 ± 5.7b

Means ± SD not followed by the same letters differ significantly (Tukey-type multiple comparison test for proportions; Zar 1996). Means are based on sum of counts per accession pooled across 28 replicates.

from that of the other four accessions. However, the proportion of winged *R. padi* on each accession was heterogeneous among replicate test pots ($\chi^2 = 200.6$, df = 135, $P < 0.001$), indicating considerable variability in antixenosis among individual plants within each accession. Neither plant height ($n = 168$, $P = 0.42$) nor dry weight of test plants ($n = 126$, $P = 0.98$) was correlated with the proportion of winged *R. padi* per plant.

Tolerance Test: Shoot Growth. The change in shoot lengths during the 7-d infestation period varied ($P < 0.05$) by accession (df = 5, 55; $F = 23.66$), aphid infestation level (df = 1, 11; $F = 34.44$), and accession-by-infestation level interaction (df = 5, 54; $F = 2.79$). Shoot lengths of Arapahoe and KS92WGRC24 wheat were limited by a 300 aphid-day infestation of *R. padi*, but shoot lengths of 8TA5L, H7089-52, and Stniism 3 triticale and MV4 wheat were not affected, indicating tolerance to *R. padi* in these latter four accessions (Table 5). Tolerance was very strong in H7089-52, as shoot lengths were virtually equivalent between the 0 and 300 aphid-day treatments.

Discussion

Antibiosis, antixenosis, and tolerance may be useful in limiting the direct effects of *R. padi* on small grains, but antibiosis and antixenosis are preferred modalities for managing *R. padi* to limit the incidence of BYDV (Kennedy 1976, Gibson and Plumb 1977, Power and

Table 5. Tolerance test: shoot growth (centimeters) over 7 d (mean ± SE) with or without *R. padi* infestation

Accession	Aphid-days	
	0	300
Arapahoe wheat	18.6 ± 0.6	13.0 ± 0.9*
8TA5L triticale	17.2 ± 0.8	15.1 ± 0.8
H7089-52 triticale	9.4 ± 0.5	9.7 ± 0.7
KS92WGRC24 wheat	16.0 ± 1.5	11.7 ± 1.2*
MV4 wheat	20.7 ± 0.7	17.8 ± 1.0
Stniism 3 triticale	13.8 ± 0.7	11.0 ± 1.3

Asterisk indicates that shoot growth differed between the 0 and 300 aphid-day treatments for plants of the same accession. Shoot growth was defined as the change in seedling height (measured from soil level to the tip of the longest leaf) during the 7-d infestation period. Aphid-days are the cumulative total of *R. padi* infestation over the 7-d infestation period. Means are for two identical tests ($n = 12$).

Gray 1995). This is because antibiosis and antixenosis limit *R. padi* population buildup and attenuate secondary spread of BYDV, whereas tolerance allows relatively large populations of *R. padi* that could increase secondary spread and incidence of BYDV (Gibson and Plumb 1977, Power and Gray 1995). In the current study, Stniism 3 demonstrated all three forms of resistance against *R. padi*, accessions 8TA5L and H7089-52 expressed antibiosis and tolerance, and MV4 wheat was tolerant to *R. padi.*

Two of the accessions have shown resistance to cereal aphids in previous studies. Nkongolo et al. (1989) found that Stniism 3 (as PI 386156) was tolerant to *D. noxia*, and Webster (1990) determined that it was tolerant, antibiotic, and antixenotic to *D. noxia.* Papp and Mesterházy (1993) found that MV4 was tolerant to *R. padi.* MV4 wheat also has shown low-level antibiosis and antixenosis to *R. padi* in some previous studies but not others (Hesler et al. 1999, 2003). It did not show antibiosis or antixenosis in the current study. Together, results with MV4 suggest large variability in its expression of antibiosis and antixenosis but relatively consistent expression of tolerance.

Few studies have been published regarding evaluation of *R. padi* resistance in triticale. Kieckhefer and Thysell (1981) found no meaningful resistance to *R. padi* among 20 triticale accessions. None of the triticale accessions in my experiments were among the 20 accessions that they tested. Neil et al. (1997) found that *R. padi* produced few offspring on 'Decade' triticale compared with that on wheat accessions. Despite relatively limited testing of triticale against *R. padi* among these studies and mine, four accessions have shown resistance. These results, coupled with known resistance of triticale to other cereal aphids, suggest that more testing for cereal aphid resistance in triticale is warranted.

Triticale is an anthroposynthetic small grain with several different groups of origin (Furman et al. 1997). Stniism 3, 8TA5L, and H7089-52 are from three different groups of origin, and therefore are likely distinct sources of resistance to *R. padi*. Stniism 3 and 8TA5L may be important sources of resistance to *R. padi* in triticale and other small grains, particularly wheat. Resistance to *D. noxia* in Stniism 3 is controlled by a single dominant gene (Nkongolo et al. 1992) with its locus on chromosome arm 4R and derived from the *Secale strictum* C. Presl (as *S. montanum*) parent (Fritz et al. 1999). However, Lukaszewski et al. (2001) concluded that transfer of *D. noxia* resistance from Stniism 3 into wheat will be difficult because of unclear genetics, low levels of chromosome homology, and structural differences between donor and recipient chromosomes and that effort to transfer resistant *Secale* chromatin from Stniism 3 to wheat may not be justified. Nonetheless, advances in molecular genetic techniques, which have the potential to facilitate introgression of insect resistance genes between cereals (Quisenberry and Clement 2002), may improve the probability of successful transfer of *R. padi* resistance traits from Stniism 3 to small grain cultivars.

The genetics of antibiosis resistance to *R. padi* in Stniism 3, 8TA5L, and H7089-52 need to be determined. It is not known whether the same or different gene(s) are responsible for the modalities resistance to *R. padi* and *D. noxia* in Stniism 3. Regardless, resistance to both of these aphid species may justify use of this accession as a breeding source for cereal aphid resistance. 8TA5L, H7089-52, and MV4 should be screened for resistance to other cereal aphids, and Stniism 3 should be screened against cereal aphids other than *R. padi* and *D. noxia.* Information on the genetics of *R. padi* resistance in these accessions and the spectrum of their resistance against cereal aphids would clarify their potential for use as resistance sources in small grain breeding programs.

Acknowledgments

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